

A NEW LATE DEVONIAN ACANTHODIAN FISH FROM MT. HOWITT, VICTORIA, AUSTRALIA, WITH REMARKS ON ACANTHODIAN BIOGEOGRAPHY

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ABSTRACT: A new acanthodiform acanthodian, *Howittacanthus kentoni* gen. et sp. nov., is described from the Frasnian laeustrine Mt. Howitt site, eastern Victoria. *Howittacanthus* is characterized by: a palatoquadrate ossified in three divisions with both otic and auxiliary otic cotyli in contact with the braincase; autopalatine with posterior basal process; slender body form with small pelvic fins closer to anal than to pectoral fins; and all fin-spines ornamented with a single ridge. Ontogenetic data obtained from *Howittacanthus* agree with the findings of Zidek (1985) for *Acanthodes*. The family Acanthodidae is redefined. *Howittacanthus* is placed as the possible sister taxon to a group containing *Acanthodes* and *Acanthodopsis* by shared characters of the jaw cartilages. A Euramerican centre of origin is proposed for acanthodiforms, gyracanthids and diplacanthoids. These groups probably entered the East Gondwana Province following faunal interchange with the Euramerican Province sometime in the Middle Devonian.

Few acanthodian fishes are known from Australia, and the only articulated complete fish come from the Late Devonian Mt. Howitt site, the Lower Carboniferous Mansfield Basin (both in Victoria), and from the Givetian Bunga Beds of New South Wales. The Mansfield Basin fauna was described by Woodward (1906) as containing three acanthodians, *Gyracanthides murrayi*, *Acanthodes australis* and *Eupleurognmus creswelli*. *Eupleurognmus* was erected on parts of the trunk squamation which showed enlarged scales flanking the lateral line. Such scales are now known to also occur on *Acanthodes* (Zidek 1976) and the genus *Eupleurognmus* cannot be substantiated. Similarly *Acanthodes australis* was not defined by unique features, and, as it is only imperfectly known from the tail, it cannot be maintained as a separate species and should be referred to as *Acanthodes* sp. Articulated acanthodians from the Bunga Beds (Fergusson *et al.* 1979) possess two dorsal fins and apparently lack dermal shoulder girdle armour. They are provisionally identified as ischnacanthids but details of the head are not preserved and the presence of gnathal bones, which characterize the Ischnacanthida, cannot be demonstrated. The Mt. Howitt acanthodians show the best preservation; the fish are preserved in finely-laminated shale which enables all aspects of their skeletal morphology to be revealed by latex casts after the friable bone is dissolved in weak hydrochloric acid. The Mt. Howitt fauna contains one of the most diverse and well-preserved assemblages of freshwater Late Devonian fishes in the world, including several species of placoderms (Long 1982, 1983a, 1984), osteichthyans (Long 1985) and acanthodians. Aside from the new acanthodiform (here used in the sense of Order Acanthodida) described in this paper one other acanthodian has been described from the fauna, a deep-bodied diplacanthoid, *Culmacanthus stewarti* (Long 1983b). Elsewhere in Australia acanthodiforms are known only from a new occurrence in the Raymond Formation, Drummond Basin, Queensland. These specimens are three-dimensionally preserved isolated bones (including

basisphenoids, scapulocoracoids and jaws) belonging to a new genus. Current preparation of new blocks of the Raymond Formation bone-bed should produce much more of this important acanthodian material for description in the near future.

Although the acanthodiforms are known from the Early Devonian to the mid Permian, the structure of the group is known primarily from one genus, *Acanthodes* (Miles 1964, 1965, 1968, 1973a, 1973b). *Acanthodes*, the most successful member of the group, flourished worldwide during the Carboniferous and Permian periods, long after most other acanthodian groups had declined. Relationships of the acanthodians, and acanthodiforms in particular, have been recently discussed by Long (in press). The new genus from Mt. Howitt is of biogeographic importance in being the earliest record of an acanthodiform which is geographically distant from the Euramerican Province (*sensu* Young 1981). It is also the first Devonian acanthodiform described from the Southern Hemisphere, and as specimens are preserved in all stages of growth the material allows some comment on the ontogenetic development of acanthodians in general.

The material was collected by Prof. J. Warren and staff and students of the Zoology Dept., Monash University, over two field seasons in the early 1970s. It was prepared by immersion in weak hydrochloric acid so that latex casts of the cleaned moulds could be made. It is housed in the Museum of Victoria, Melbourne (NMV).

SYSTEMATIC PALAEOONTOLOGY

- Subclass ACANTHODII
Order ACANTHODIFORMES
Family ACANTHODIDAE

DIAGNOSIS: Acanthodiform acanthodians which have an elongated gill chamber with very small, thin branchiostegals that extend only halfway across the length of the gill chamber. Pelvic fins small relative to pectorals.

REMARKS: Miles (1966) distinguished this family from the two other acanthodid families (Mesacanthidae and Cheiracanthidae) by possession of six characters. As some of these are also found in mesacanthids or cheiracanthids (e.g. lack of intermediate fin-spines, pectoral fin-spine of great length relative to body length in *Cheiracanthus*; scales with unornamented flat crown in mesacanthids), I have amended the diagnosis to include only derived characters of acanthodids. In addition to these characters, acanthodids often have the following features: pelvic fin-spines situated closer to pectoral fin than to anal fin; procoracoid with two attachment areas to scapulocoracoid; all fin-spines with single rib ornamentation. The new genus is referred to this family by having very small, slender branchiostegal rays, and, in addition, has a single rib on each fin-spine.

Denison (1979) did not recognize Miles' (1966) division of the order Acanthodida into three families, instead preferring to retain all genera in one family, Acanthodidae, because of the lack of recognizable synapomorphies defining these families. Mesacanthids appear to lack characteristic specializations, and are currently defined (Miles 1966) on plesiomorphic acanthodian features (presence of intermediate fin-spines; well-developed branchiostegal rays etc.). Some cheiracanthids exhibit synapomorphies; these are discussed in the phylogenetic section of this paper. Mesacanthidae therefore cannot be maintained as a valid family but should be regarded as a plesiomorphic sister group to the two definable acanthodid families, Cheiracanthidae and Acanthodidae.

Howittacanthus gen. nov.

1976 acanthodiforms; Marsden, p. 122

1982 Acanthodiformes; Long, p. 63.

1983a acanthodiform acanthodians; Long, p. 298

1983b acanthodiforms; Long, p. 51.

1983c *Acanthodes*-like acanthodian; Long, p.23, fig. 9.

1984 cf. *Acanthodes* sp.; Long & Turner, p. 240.

ETYMOLOGY: After Mt. Howitt where the specimens were found, and the Greek "acanthos", spine.

DIAGNOSIS: Slender acanthodid acanthodian reaching a maximum length of about 25 cm. Pelvic fin-spines half as long as the pectoral fin-spines and situated closer to the anal fin than to the pectoral fin. External length of dorsal fin-spine shorter than anal fin-spine, and all spines ornamented with one thick rib. Meekelian bone ossified as a single unit; palatoquadrate ossified as three divisions with otic and auxiliary otic cotyli present. Autopalatine with basal process in posterior half. Scapular short without suprascapular ossification. Procoracoid small and slender. Scales without ornament on the crown.

TYPE SPECIES: *Howittacanthus kentoni* sp. nov.

REMARKS: This acanthodid is distinguished from all others except *Acanthodes* and *Acanthodopsis* by having

the dual otic cotyli on the palatoquadrate, and *Acanthodopsis* is readily distinguished by the presence of teeth on the jaws (see Long in press, for a discussion of the systematic position of this genus). *Howittacanthus* is distinguished from *Acanthodes*, *Pseudacanthodes* and *Traquairichthys* by the placement of the pelvic fin closer to the anal fin (and by its absence in *Traquairichthys*). *Howittacanthus* closely resembles *Protogonacanthus* by its body shape and fin placement but differs in having singularly-ribbed fin-spines. Although *Carycinacanthus* is poorly known, it can be distinguished from *Howittacanthus* by the shape of the tail and ratio of anal fin-spine to dorsal fin-spine length.

Howittacanthus kentoni sp. nov.

Figs 1-6, 7A, 8, 9, 10E.

ETYMOLOGY: In honour of Prof. K. S. W. Campbell, Geology Dept., Australian National University for his contribution to the study of early vertebrates.

DIAGNOSIS: as for genus, only species.

MATERIAL: Holotype, NMV P179580, a complete individual (Figs 1A, 2). Paratypes, NMV P179582 (Figs. 1B, 4B, 5C) and NMV P179591 (Fig. 3E), showing details of the head. NMV P179570-P179629, individuals in various stages of growth.

LOCALITY AND AGE: Mt. Howitt Spur quarry, lower part of the Avon River Group (Long 1983a, Fig. 1). Late Devonian (Frasnian).

DESCRIPTION: *Howittacanthus* is a medium-sized acanthodid with a fusiform shape as in other genera. The head occupies one-sixth of the total length of the fish and the body had a depth/length index (x100) close to 13 in mature individuals. Proportions of fin-spine lengths to body lengths are shown in Table 1.

The head contained internally ossified jaw cartilages and gill rakers, and dermal sclerotic ring bones. The dorsal surface of the head was covered with small tesserae (tss, Fig. 4B) which are slightly larger than surrounding scales. On one large specimen, NMV P179598 (Figs. 3F, G, 4C, D), the lateral face of the dorsal ossification of the braincase is preserved, and therefore, the absence of the braincase in smaller specimens presumably indicates that it was only fully ossified in large individuals. All other skeletal elements in the head were presumably cartilaginous (gill arch bones and possibly endocranial components). The lateral face and part of the dorsal surface of the dorsal ossification of the braincase (end) can be seen in NMV P179598 (Figs 3, 4). It has a relatively small otic condyle (con) and large auxiliary otic condyle (a.con) on the ascending process. A depression on the dorsal surface, just anterior to the ascending process may be an anterior fontanelle (?fon) as occurs in *Acanthodes* (Miles 1973b).

The palatoquadrate has three separate ossifications, quadrate (Qd), metapterygoid (Mpt) and autopalatine (Aut), as in *Acanthodes* (Miles 1973b, Zidek 1980). Although the jaws of *Howittacanthus* are similar to those of *Acanthodes*, a comparison between the two (Fig. 7) shows that *Howittacanthus* differs in the relative

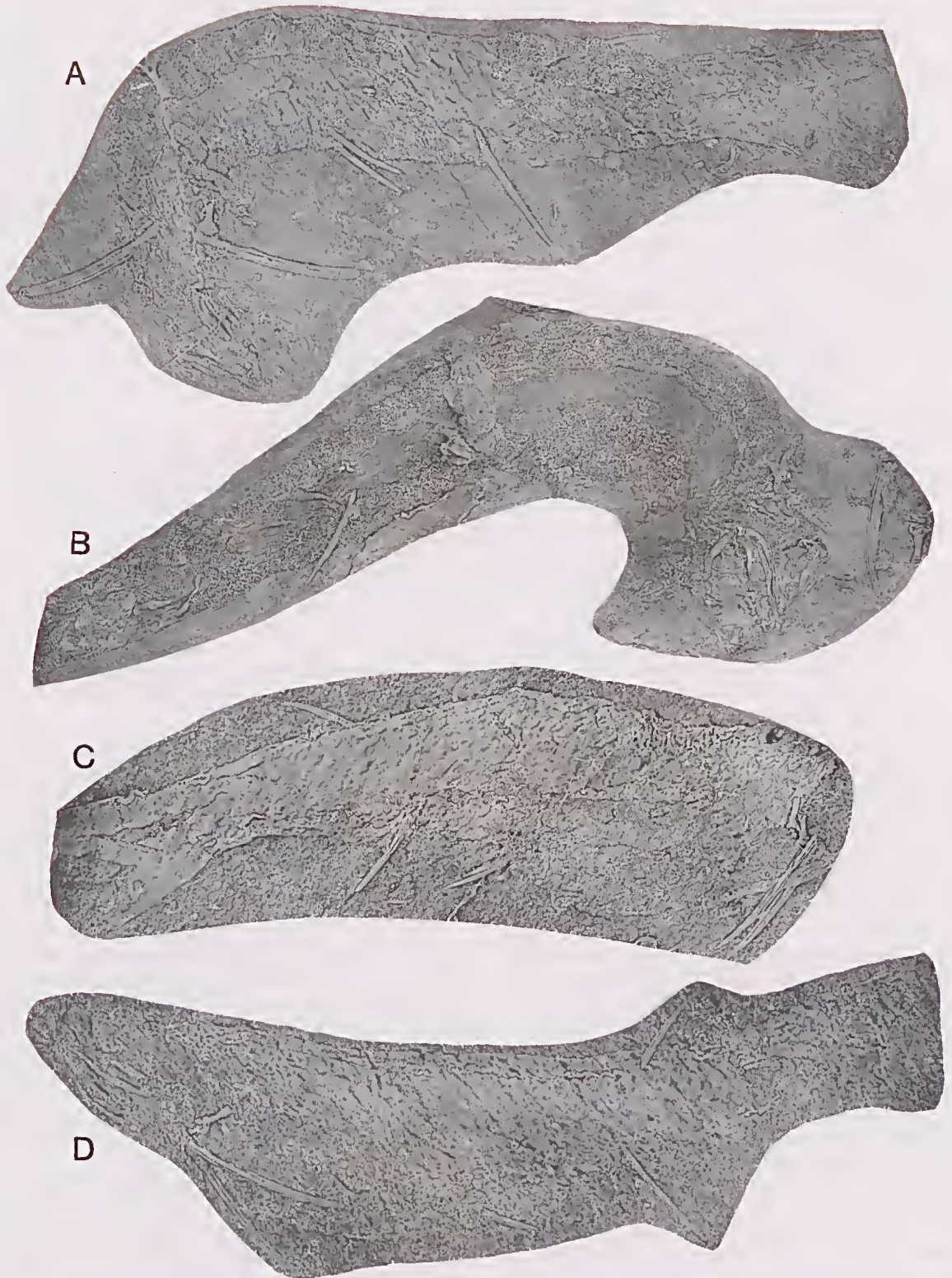


Fig. 1—*Howittacanthus kentoni* gen. et sp. nov., Late Devonian, Mt. Howitt, Victoria. A, holotype, NMV P179580 (X1). B, Paratype, NMV P179582 (X1). C, NMV P179572 (X1.8). D, NMV P179571 (X1.5). Latex casts whitened with ammonium chloride.

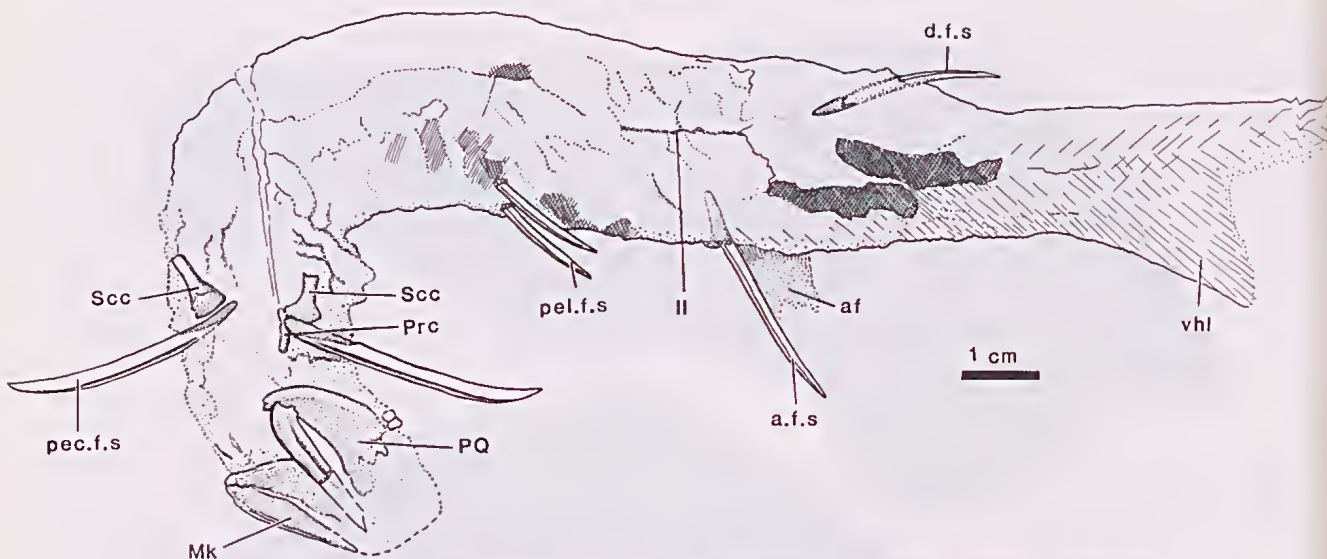


Fig. 2—*Howittacanthus kentoni* gen. et sp. nov., Late Devonian, Mt. Howitt, Victoria. Sketch of holotype, NMV P179580, showing main features. a.con—auxiliary articular condyle; af—anal fin; afs—anal fin spine; a.ot.c—auxiliary otic cotylus; Aut—Autopalatine; ax.l—axial lobe of tail; bas—basal process of autopalatine; BR—branchiostegal rays; con—articular condyle; der—dermal fin ray supports; df—dorsal fin; d.f.s—dorsal fin-spine; dhl—dorsal hypochochordal lobe of tail; dl—dorsal lateral line; end—endocranium (dorsal ossification); epr—exopalatoquadrate ridge; fon—dorsal endocranial fontanelle?; gc—gill chamber; hy—foramen for hyoideus trigeminus nerve; hym—hyomandibular; II—lateral line; man.b—mandibular bone or splint; mes.l—mesial lamina of scapulo-coracoid; Mk—meckelian cartilage; Mpt—Metapterygoid; na—circum nasal bone?; ot.c—otic cotylus; pec.f.s—pectoral fin-spine; pel.f—pelvic fin; pel.f.s—pelvic fin-spine; PQ—Palatoquadrate; Prc—Procoracoid; Qd—Quadrate; See—Scapulo-coracoid; scl—sclerotic bones; tss—cranial tesserae; vhl—ventral hypochochordal lobe of tail; vl—ventral sensory line; z1-z4—zones of caudal squamation (after Heyler, 1969).

sizes of metapterygoid to autopalatine bones, the stronger development of a ridge behind the cotyli on the metapterygoid, in the position of the basal process (bas) on the dorsal margin of the autopalatine, and in the shape of the anterior end of the meckelian cartilage (Mk). The quadrate and metapterygoid are closely associated with only a small cartilaginous gap between them which closes up in large individuals (e.g. NMV P179598). The quadrate, the largest of the three upper jaw ossifications, is rather featureless apart from the well-developed extrapalatoquadrate ridge (epr). This continues onto the metapterygoid to terminate as a thickening behind the otic and auxiliary otic cotyli which encloses a foramen, presumably for the ramus hyomandibularis trigemini nerve. The autopalatine is elongated with a strongly-developed basal process situated closer to the posterior end of the bone as opposed to that of *Acanthodes* which forms the anterodorsal corner of the bone (Fig. 7). The metapterygoid and autopalatine ossifications are approximately the same size. The mandibular joint can only be seen in lateral view but appears to be of the normal *Acanthodes*-type with strongly-developed prearticular and articular processes on the quadrate (Miles 1973b, Long in press). The meckelian cartilage was perichondrally ossified as a single unit (NMV P179600, Fig. 5B) and was strengthened by a dermal mandibular splint (man.b) which lies on the ven-

tro-lateral edge of each jaw ramus. The mandibular splint bears ornamentation of short ridges and grooves oriented posteroventrally to near horizontal in its central section. The anterior end of the meckelian bone is broad with a short straight anterior margin which has a circular symphyseal facet for ligamentous attachment of the opposing jaw (NMV P179598, NMV P179600; Fig. 5B) similar to that in *Acanthodes hundi* (Zidek 1980).

The gill arch rakers (gr) are small conical bones which are found in linear array behind the jaw ossifications (Fig. 4A). They are proportionally smaller than for *Acanthodes* (Zidek 1976, 1980). The branchiostegal rays (BR) are very slender bones which can be seen in several specimens coming from behind the jaw cartilages. The number of rays is hard to estimate as most specimens have the head slightly disrupted with branchiostegals scattered. The number is relatively low compared to *Acanthodes*, and probably similar to *Homalacanthus* (Miles 1966).

The sclerotic ring (scl) is composed of five dermal bones each bearing a very fine ornament of minute tubercles. The anterodorsal and posterodorsal sclerotic bones are the largest elements and these are broader at their contact margin with each other, at the top centre of the ring, than at their ventral borders. The diameter of the whole sclerotic ring when restored is just under half the length of the palatoquadrate.

The endoskeletal shoulder girdle has two ossifications, a short scapulocoracoid (Sec) and a small procoracoid (Prc). There is no evidence in any of the specimens for a dorsal suprascapular ossification as found in *Acanthodes*. The scapulocoracoid (Figs 2, 3A, C, D, E, 4A, 6A, B, D, E) has a slender dorsal division and an expanded ventral mesial lamina (mes. 1) which has a ventral groove for the pectoral fin-spine. The procoracoid (Figs 2, 3C, E, 4A) is a slender curved bone which sits underneath the fin-spine in anterior contact with the scapulocoracoid. The scapulocoracoid is about twice as high as the breadth of the ventral division, with the procoracoid being about two-thirds as long as the long axis of the scapulocoracoid. The fin-spine sat within the ventral groove of the scapulocoracoid which has a well-developed descending mesial lamina that flanks the fin-spine. No foramina are visible on the scapulocoracoid. Overall the pectoral girdle is at a similar level of organization to that of *Cheiracanthus* (Miles 1973a).

All the fin-spines have a single, thick, longitudinal rib along their leading edge, separated from the sides of the spine by well-defined lateral grooves. The fin-spines are quite flat with short, concave posterior faces and

finely-striated insertion areas. The pectoral fin-spine (pec.f.s) is approximately the same size as the anal spine (a.f.s) but considerably broader. The pelvic spines (pel.f.s) are about half as long as the anal spine; the dorsal spine (d.f.s) being only marginally shorter than the anal spine.

The fin webs are partially preserved on some specimens (Figs 1, 2, 5D) permitting estimation of the complete fin shape (Fig. 9B). The pectoral fin (pec.f) is narrow-based with strong radial lineation of the scale rows close to the body. The pelvic fin (pel.f) is long-based, extending back almost to the start of the anal fin, a condition usually found in higher acanthodids such as *Acanthodes* (Zidek 1976) and *Pseudacanthodes* (Denison 1979). Both the dorsal (df) and anal fins (af) are poorly preserved, but appear to run in a straight line back from the tip of the fin-spine to the body to give a broad-based triangular outline.

The caudal fin is well preserved on a few specimens (NMV P179581, P179618; Figs 5A, D, 8). The main axis of the body continues in a straight line to form the axial lobe of the tail, without the tail being angled away from the fusiform body. The axial lobe is very long as it takes

TABLE 1
PROPORTIONS OF *Howittacanthus kentoni* GEN. ET SP. NOV., COMPARED WITH THOSE OF *Acanthodes bridgei* AND *A. lundi* (DATA AND MEASURING POINTS FROM ZIDEK, 1985). n, number of specimens measured.

	n	average	range	<i>A. bridgei</i>	<i>A. lundi</i>
(a) $\frac{\text{Pectoral-anal distance}}{\text{Total specimen length}}$	8	0.43	0.38-0.47	0.42-0.51	0.46-0.52
(b) $\frac{\text{Pelvic-anal distance}}{\text{Total specimen length}}$	8	0.16	0.13-0.21	0.28-0.37	0.38-0.47
(c) $\frac{\text{Prepectoral length}}{\text{Total specimen length}}$	3	0.17	0.13-0.19	0.18-0.24	0.21-0.29
(d) $\frac{\text{Pectoral spine length}}{\text{Total specimen length}}$	7	0.15	0.14-0.17	0.17-0.20	0.15-0.20
(e) $\frac{\text{Pelvic spine length}}{\text{Total specimen length}}$	7	0.065	0.06-0.07	0.07-0.08	0.05-0.06
(f) $\frac{\text{Dorsal spine length}}{\text{Total specimen length}}$	6	0.11	0.10-0.12	0.12-0.14	0.12-0.13
(g) $\frac{\text{Anal spine length}}{\text{Total specimen length}}$	6	0.13	0.12-0.14	0.12-0.14	0.11-0.16
(h) $\frac{\text{Pelvic spine length}}{\text{Pectoral spine length}}$	7	0.44	0.41-0.46	0.17-0.20	0.27-0.35
(i) $\frac{\text{Dorsal spine length}}{\text{Pectoral spine length}}$	5	0.67	0.57-0.75	0.64-0.74	0.62-0.63
(j) $\frac{\text{Anal spine length}}{\text{Pectoral spine length}}$	5	0.80	0.71-0.88	0.64-0.74	0.72-0.77

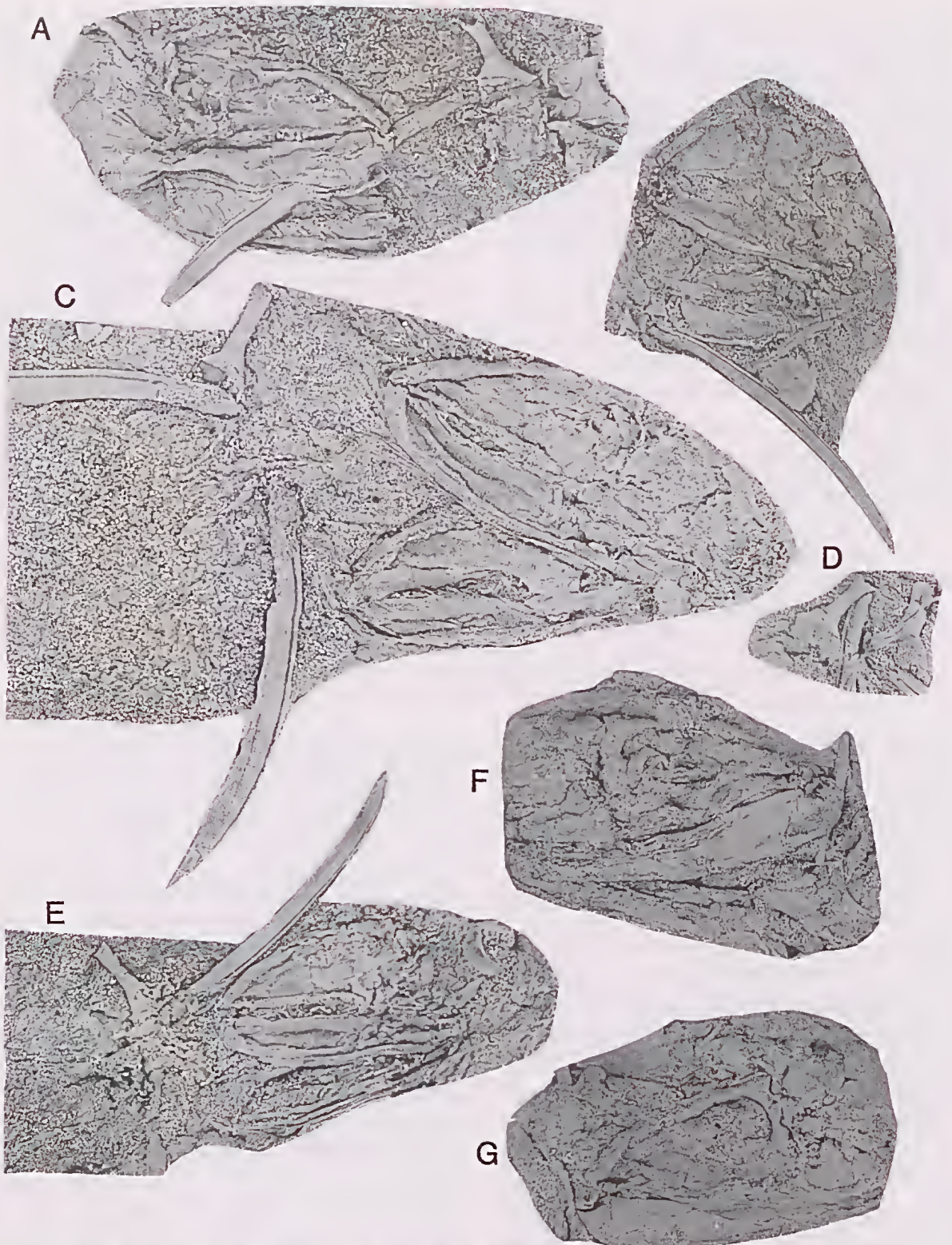


Fig. 3—*Howittacanthus kentoni* gen. et sp. nov., Late Devonian, Mt. Howitt, Victoria. A, NMV P179593 (X2.3). B, NMV P179590 (X2). C, NMV P179586 (X2.5). D, NMV P179603 (X2). E, paratype, NMV P179591 (X2). F, G, lateral views of each side of NMV P179598 (X1.9). Latex casts whitened with ammonium chloride.

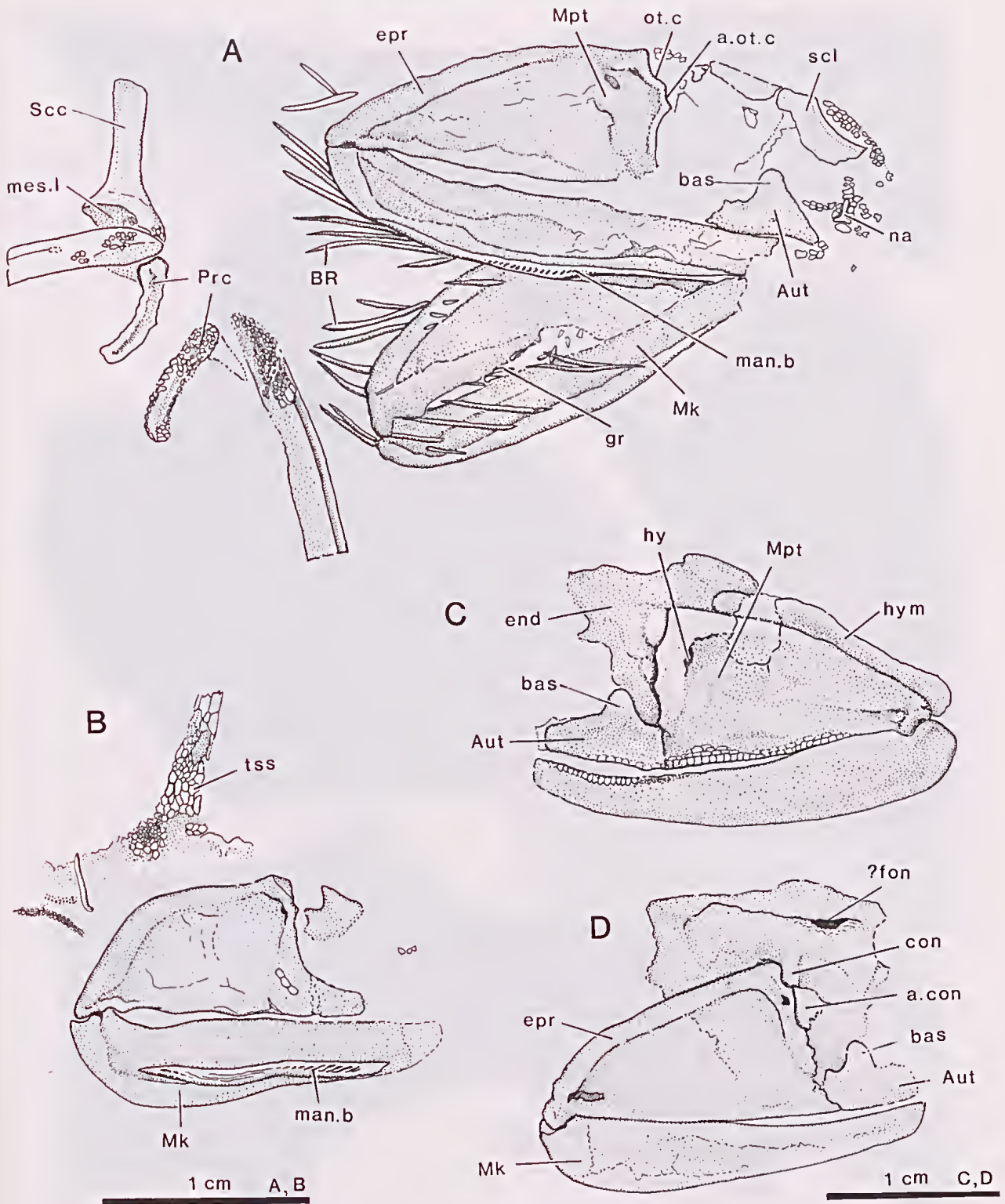


Fig. 4—*Howittacanthus kentoni* gen. et sp. nov., Late Devonian, Mt. Howitt, Victoria. Details of the head and shoulder girdle. A, NMV P179586. B, paratype, NMV P179582. C, D, both sides of NMV P179598. See legend to Fig. 2 for abbreviations.

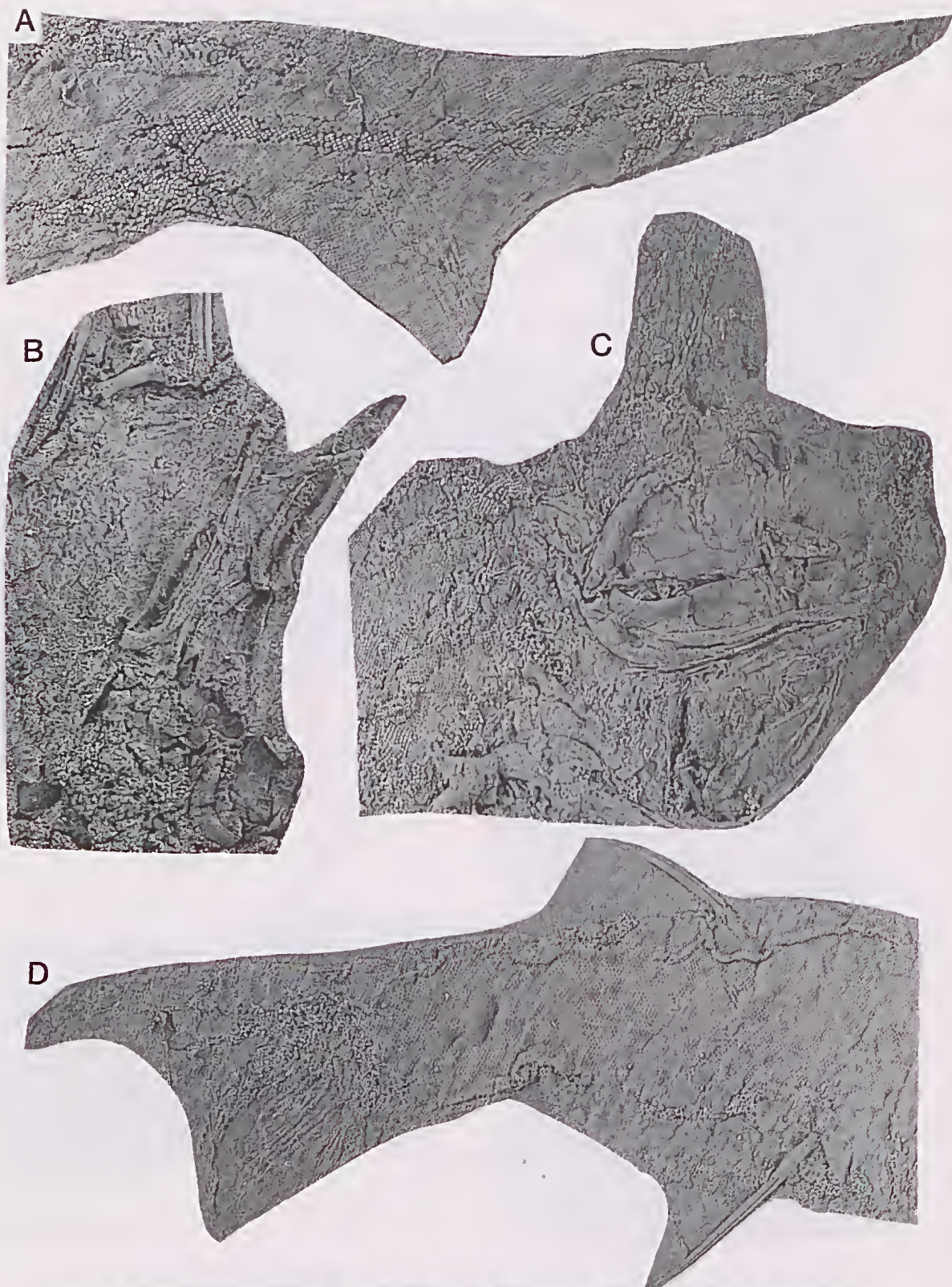


Fig. 5—*Howittacanthus kentoni* gen. et sp. nov., Late Devonian, Mt. Howitt, Victoria. A, tail of NMV P179581 (X2.6). B, NMV P179600 (X2.4). C, paratype, NMV P179582 (X3). D, tail of NMV P179618 (X2.4). Latex casts whitened with ammonium chloride.

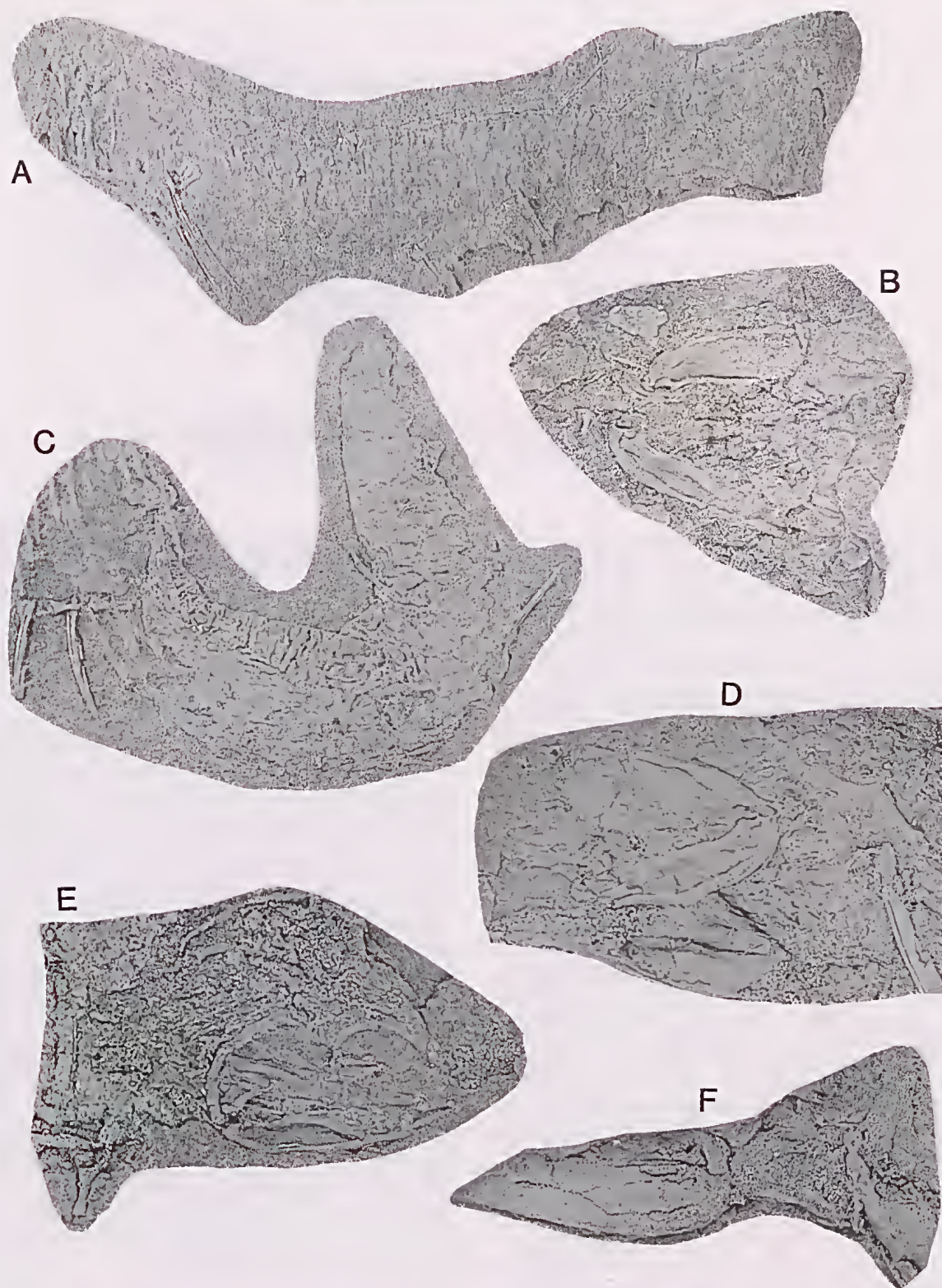


Fig. 6—*Howittacanthus kentoni* gen. et sp. nov., Late Devonian, Mt. Howitt, Victoria, A, NMV P179576 (X2). B, NMV P179579 (X2.6). C, NMV P179585 (X1.5). D, NMV P179616 (X2). E, NMV P179589 (X1.9). F, NMV P179599 (X2). Latex casts whitened with ammonium chloride.

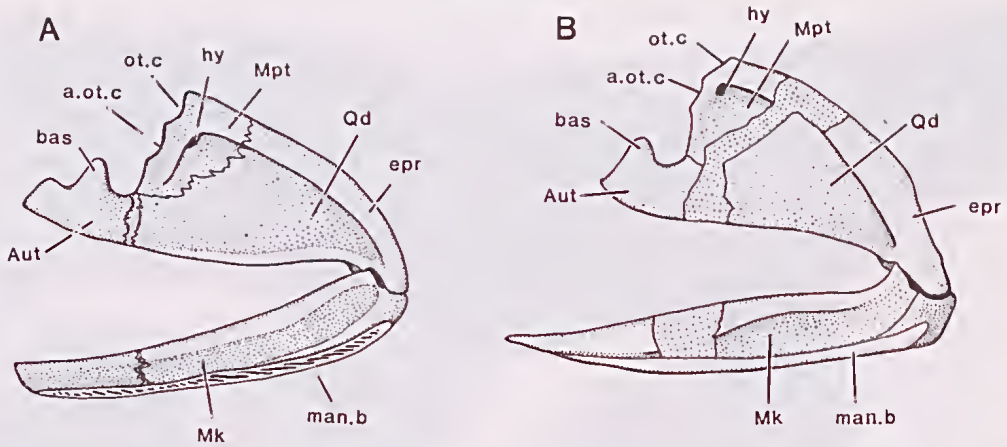


Fig. 7—Comparison between the reconstructed jaws of A, *Howittacanthus kentonii* gen. et sp. nov., and B, *Acanthodes bronni* (after Miles, 1973a). Note particularly the shape of the autopalatine and anterior end of the meckelian cartilage. See legend to Fig. 2 for abbreviations.

up approximately one quarter of the total length of the fish. The ventral hypochordal lobe of the tail is relatively short, extending outwards from the main axis of the body for only a third of the length of the axial lobe of the tail. In NMV P179581 (Figs 5A, 8) the squamation of the tail is very well preserved, and shows some Z2 scales present near the base of the main lobe, and development of an additional Z2' zone (as defined by Heyler 1969, also Zidek 1976). Development of Z1, Z3 and Z4 scales are as in *Acanthodes*. Z2' scales are only found on mature specimens (in *Acanthodes*, Zidek 1976) and thus indicate that NMV P179581 represents the mature condition of *Howittacanthus*. At least two specimens (NMV P179581, P179618) show linear ridges (der) radiating out from the main axis of the body to strengthen the ventral hypochordal lobe. These are undoubtedly fin-ray supports or caudal hypurals as described in *Acanthodes* by Miles (1970), although the exact number (at least 9 in NMV P179618) cannot be determined in *Howittacanthus*. The scales of *Howittacanthus* are typically acanthodid and are very small, with a flat, unornamented, rhombic crown, and relatively shallow base, but are indistinguishable from those of *Acanthodes* since the histology of the *Howittacanthus* scales remains unknown.

The laterosensory system is well developed in *Howittacanthus*. The main lateral-line (ll) can be seen running midway along the body depth in many specimens (e.g. Fig. 5D), represented by slight displacement of the scales which forms a ridge along the body surface. A dorsal sensory-line (dl) can be seen as a thick ridge of displaced scales running in irregular fashion close to the anterior margin of the body from the head to just behind the dorsal fin. This feature is most pronounced in juveniles (e.g. NMV P179576, 179572, 179571, 179618; Figs 1C, D, 5D, 6A, B). Little of the sensory-line system can be made out on the head

although some specimens show segments of the preopercular and mandibular lines (e.g. NMV P179598, 179599, Fig. 6F; 179582, Fig. 5C). A ventral sensory line (vl) is also present, seen on NMV P179603 and 179570.

ONTOGENETIC DEVELOPMENT OF *HOWITTACANTHUS*

Measurements were taken only on specimens that clearly showed the particular parameter to be measured, so, although the sample size is small for stated proportions, they are an accurate summary of the range of variation shown by the material. Points used for measurements followed Zidek (1976). Zidek's (1985) recently-published account of the ontogenetic variation exhibited in two species of *Acanthodes* formed the basis for a similar investigation of these ratios in *Howittacanthus*.

The morphology of juveniles does not differ from mature individuals but certain proportional changes occur during ontogeny. Table 1 summarizes proportions for the growth of body sections and fin-spines relative to total length. These findings agree with Zidek's results for *Acanthodes* that the ratios are constant throughout growth, and hence are reliable for use in species diagnosis. Similarly, the ratios of the length of the mandible (meckelian cartilage plus mandibular splint) remains constant at 9-11% total body length, or 18-22% of the pectoral-anal distance. The scapulocoracoid/pectoral fin-spine ratio was also constant through growth, ranging from 22-29% (av: 26%). In the few specimens which permit accurate estimation of the sclerotic ring diameter this was found to be approximately 10% of the pectoral-anal distance, also being constant throughout growth.

Preservation of very small individuals shows that the scale cover was complete over the body on juveniles, rather than absent from the anterior trunk region (Zidek

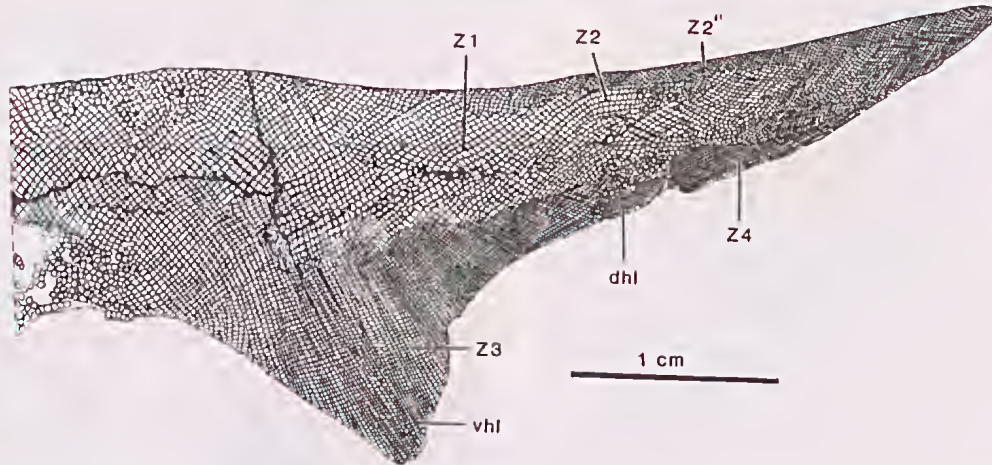


Fig. 8—*Howittacanthus kentoni* gen. et sp. nov., Late Devonian, Mt. Howitt, Victoria. Tail squamation of NMV P179581 (also in Fig. 5A). See legend to Fig. 2 for abbreviations.

1976). The head may have lacked scale cover as it is rarely preserved on the smallest individuals.

RELATIONSHIPS OF *HOWITTACANTHUS*

Long (in press) has discussed the interrelationships of acanthodians, which includes some of the better known acanthodiform genera. Fig. 11A presents a new cladogram of acanthodiforms that includes *Howittacanthus*. Interrelationships of acanthodiforms are difficult to assess because of the high degree of homogeneity in the group. Some of the characters which define the more advanced acanthodiform genera must be regarded as parallelisms which have developed independently in other acanthodian groups (e.g. presence of a procoracoid or loss of one, degree of ossification of the palatoquadrate, reduction of branchiostegal rays).

Howittacanthus is regarded as being more specialized than mesacanthids in having lost the intermediate fin-spines and more specialized than *Cheiracanthus* in having reduced branchiostegal rays. As discussed above, the mesacanthids are here regarded as a plesiomorphic group which is not characterized by any recognizable synapomorphy. Amongst the Cheiracanthidae (Miles 1966), only two genera, *Cheiracanthus* and *Homalacanthus* (Fig. 10G), appear to share synapomorphies. Within the Acanthodida, only these two genera possess scales with several ornamental ribs on the crown, and have lost the dermal mandibular splint. The recognition of these features as synapomorphies assumes that primitively, acanthodiforms possessed scales with flat unornamented crowns (as in mesacanthids and all Acanthodidae), and that the mandibular splint was primitively present in acanthodians (as it is in most climatiforms, ischnacanthids and acanthodiforms). Primitive characters of cheiracanthids (here including only the two genera under discussion) which are retained are the

presence of a procoracoid in *Cheiracanthus* (or alternatively the loss of one in *Homalacanthus*), and a singular ossification of the meckelian cartilage. Autapomorphic features are the preopercular bone in *Homalacanthus* and the anterior position of the dorsal fin in *Cheiracanthus*.

Within the Cheiracanthidae, as defined by Miles (1966), there are two or three genera which do not show derived characters in common with the two genera discussed above, nor any acanthodid synapomorphies as outlined in the amended familial diagnosis above. These taxa (*Carycinacanthus*, *Protogonacanthus*, and perhaps *Acanthodes ovensis*; Fig. 10C, D, F) should be placed as *incertae sedis* until more knowledge of their anatomy comes to hand. They are clearly more specialized than mesacanthids in lacking intermediate fin-spines, and more so than *Cheiracanthus* in the reduction of their branchiostegal rays, and on these characters I have placed them on the cladogram as the sister group of *Howittacanthus*, *Acanthodes*, and *Acanthodopsis* (with *Pseudacanthodes* and *Traquairichthys* tentatively included).

Acanthodes and *Howittacanthus* are the best known taxa within the Acanthodidae, with *Pseudacanthodes* and *Traquairichthys* undoubtedly belonging to the family but relatively poorly known (Denison 1979, Jensen 1975). *Acanthodopsis* is referred to the Acanthodidae by Long (in press) on shared characters of the metapterygoid and mandibular joint. *Howittacanthus* uniquely shares with *Acanthodes* and *Acanthodopsis* a metapterygoid with both otic and auxiliary otic cotyli, and a palatoquadrate ossified in maturity as three separate parts. Other typical acanthodid features of *Howittacanthus* are the singularly-ribbed fin-spines and partial ossification of the braincase (otherwise seen only in *Acanthodes* and here regarded as a possibly derived condition). I conclude that *Howittacanthus* is the sister group to *Acanthodes* plus *Acanthodopsis* (and tentatively *Traquairichthys* and

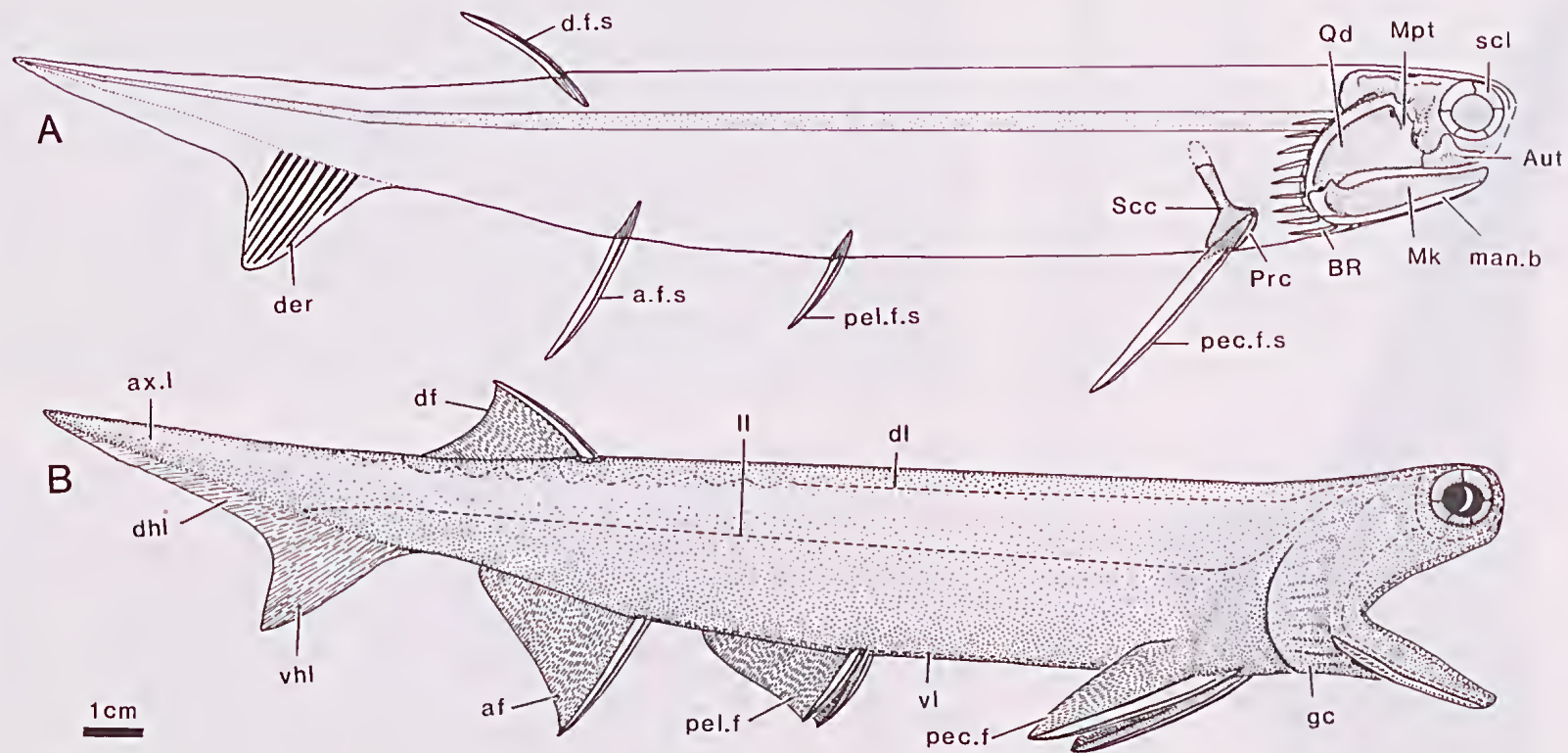


Fig. 9—*Howittacanthus kentoni* gen. et sp. nov., Late Devonian, Mt. Howitt, Victoria. A, attempted reconstruction of the fish showing known ossifications of the body (fin ray supports not actually seen). B, attempted life restoration of the fish in feeding position with mouth open. See legend to Fig. 2 for abbreviations.

Pseudacanthodes). *Traquairichthys* and *Pseudacanthodes* are derived acanthodids which share with *Acanthodes* specialization of the pelvic fin: anterior position of the pelvic fin (*Pseudacanthodes*) or loss of the pelvic fin entirely (*Traquairichthys*). Until more is known of the jaw structures in these genera I suggest that they be placed tentatively as the sister group to *Acanthodes*, *Howittacanthus* and possibly *Acanthodopsis* as they show reduction of the brachioistegal rays and elongated gill chambers. *Acanthodes ovensi*, recently redescribed by Forcy and Young (1985), does not show the characteristic placement of the pelvic fin closer to the pectoral as in other species of that genus (*A. bridgei*, Zidek 1976; *A. sulcatus*, Miles 1971; *A. lundi*, Zidek 1980). *Acanthodes ovensi* differs from all other acanthodids except *Acanthodes* and *Pseudacanthodes* by its relatively long pelvic fin web, and from these genera by the position of the pelvic fin-spine, and should probably be referred to a new genus.

SOME COMMENTS ON ACANTHODIAN BIOGEOGRAPHY

Until recently our knowledge of Gondwana acanthodians was poor, and little could be said of their zoogeographic significance. Young (1984) discussed the underlying assumptions and criticisms of Palaeozoic vertebrate zoogeography. The aim of this discussion is to utilize available palaeogeographic data (continental reconstructions based on empirical geological data) in an hypothesis to explain the known distribution of certain acanthodians. Any inferences to area connections can only be tentative in the light of changing and dissimilar views of Palaeozoic continental reconstructions (e.g. Scotese *et al.* 1979, Heckel & Witzke 1979, Riekard & Belbin 1980). Phylogenetic analysis of the Acanthodii, considered in relation to area cladograms, should then suggest where paraphyletic "stem groups" may have originated. The evidence for such an analysis is based on the known occurrence of species in time and space, and recognizable absences of taxa from sites which contain diverse and well-preserved faunas. Biogeographic provinces proposed by Young (1981) are referred to in this discussion.

The oldest reliable report of acanthodians comes from the Early-Middle Silurian of China (Pan Jiang 1983). The Ordovician acanthodian spine from Girvan, Scotland (Harper 1979) has been queried by Dr. Alex Ritchie and may be arthropodan (Blicek *et al.* 1984, p. 854). The Silurian distribution of acanthodians indicates that the group was then widespread, occurring in the Euramerican Province (Gross 1947), South China Province, East Gondwana (south-eastern Australia, Turner & Pickett 1982) and possibly from central Gondwana and the Birman Block (age not certain; Blicek *et al.* 1984, Gupta & Turner 1973). All of these occurrences include "*Nostolepis*"-type scales. Only ischnacanthid and climatiform acanthodians have been recorded from the Silurian.

The acanthodiforms first appear in the Lower Devonian of Britain and Scotland (Watson 1937, Miles 1973a), represented by one genus, *Mesacanthus*, from facies indicative of fresh water habitats (Allen & Tarlo 1963). Diverse, well-preserved faunas of Lower Devonian age from China suggest the group was absent from this region (e.g. Wang Nienzhong 1984), although few faunas of this age (and facies) are known from Australia. In this case, the absence of acanthodiforms from the East Gondwana Province during the Lower Devonian cannot be confirmed, although they appear to be absent from the *Wuttagoonaspis*-fauna reported by Ritchie (1973) and Turner *et al.* (1981). *Mesacanthus* has been shown above to be one of the plesiomorphic "stem group" acanthodiforms. Middle Devonian acanthodiforms are also restricted to the same biogeographic province, Euramerica, but are more diverse (*Cheiracanthus* spp., *Mesacanthus* spp., plus indet. scales such as *Acanthodes? dublinensis*; Gross 1973, Denison 1979). Thus the earliest and most plesiomorphic acanthodiforms as currently known appear to be endemic to the Euramerican Province, and a centre of origin for the group would be expected here. In the early Late Devonian the group is recorded for the first time from a definite marine habitat (*Protogonacanthus*, Bergisch-Gladbach limestones, Germany, Miles 1966), and from an area geographically widely separated from the earlier Euramerican occurrences (East Gondwana Province, *Howittacanthus*). These two events may be causally related: invasion of marine habitats followed by dispersal and then re-entry into new freshwater habitats. Acanthodid distribution during the Late Devonian-Permian appears to represent a simple progression-rule type of dispersal following a long period of endemism in Euramerica. *Acanthodes* (Carbo-Permian) is the first widespread genus known to occur in both marine and continental facies (Zidek 1976, Denison 1979). Apart from Euramerica, this genus is known to occur from Gondwana (South Africa, Gardiner 1973; Australia, Woodward 1906) and South China (Wang & Turner 1985), although doubt must be cast on the last of these reports as it is based on scales alone. Fig. 11B shows a schematic biogeographic history of the acanthodiforms, which clearly illustrates the widespread dispersal of the higher acanthodids during the Late Devonian and Carboniferous.

Climatiforms and ischnacanthids are widespread at their earliest appearance and flourished during the Lower Devonian particularly in Euramerica and Baltica (Miles 1973a, Bernacsek & Dinley 1977, Schultze & Zidek 1982). The diplacanthoid climatiforms are common in the Middle Devonian in Euramerica (*Diplacanthus* spp.) where they survived on to the Late Devonian (*D. horridus*, Frasnian). By the start of the Late Devonian they were also in East Gondwana, represented by a highly specialized genus, *Culmacanthus* (Long 1983). Culmacanthid cheek plates belonging to other species are now known also from the Pambula River fauna (south coast N.S.W.) and from the Devonian of Antarctica (Dr. G. Young, pers. comm.) indicating that they are probably an endemic East Gondwana group.

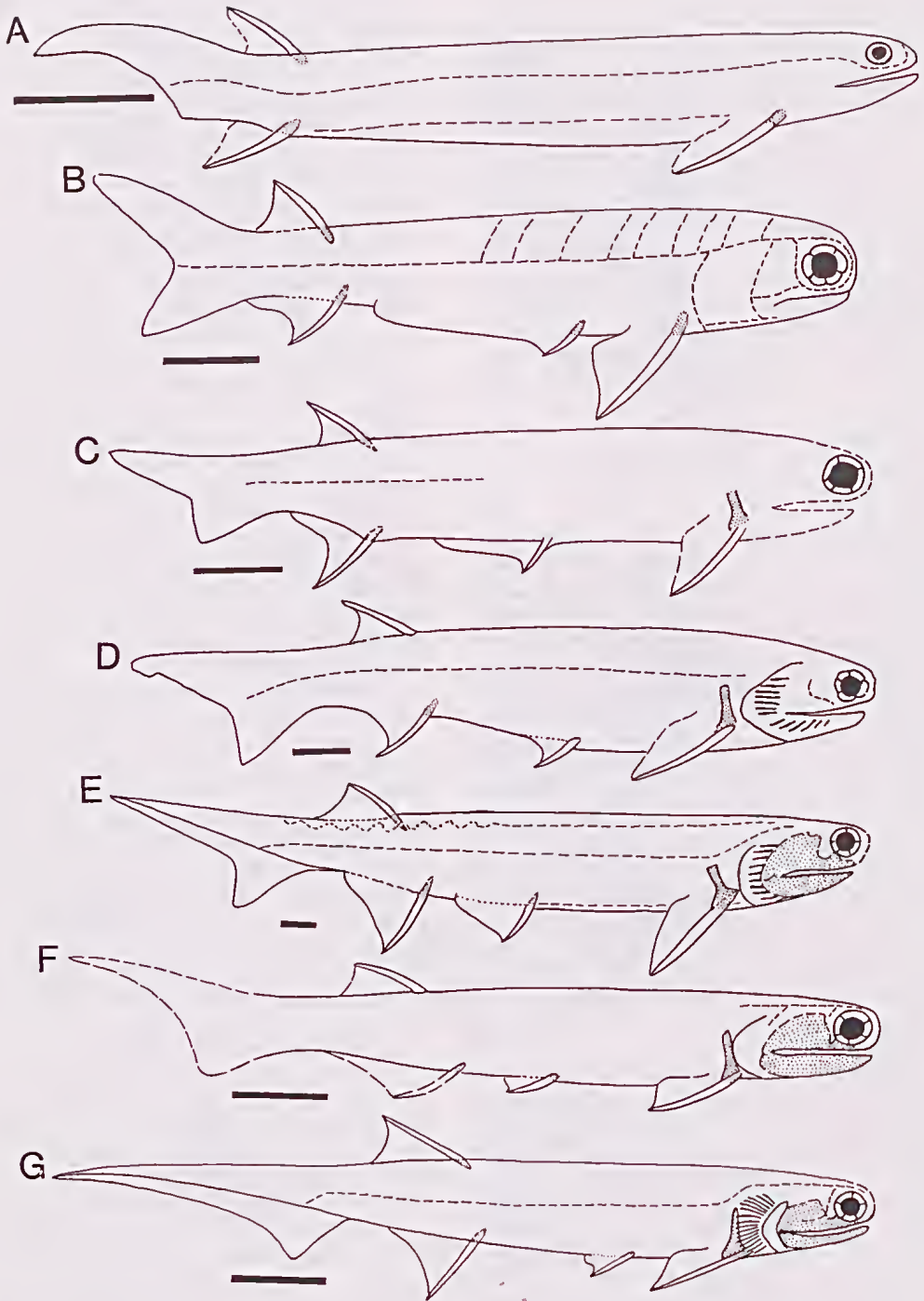


Fig. 10—Comparison of body morphology of certain higher acanthodiforms. A, *Pseudacanthodes* (Late Carb., Europe). B, *Acanthodes bridgei* (Late Carb., U.S.A.). C, *Acanthodes ovensi* (Early Carb., Scotland). D, *Carycinacanthus* (Early Carb., U.S.S.R.). E, *Howittacanthus* (Late Dev., Australia). F, *Protogonacanthus* (Late Dev., Europe). G, *Homalacanthus* (Late Dev., Canada). All except C and E after Denison (1979). C, after Forey & Young (1985). E, original. One centimetre bar scale.

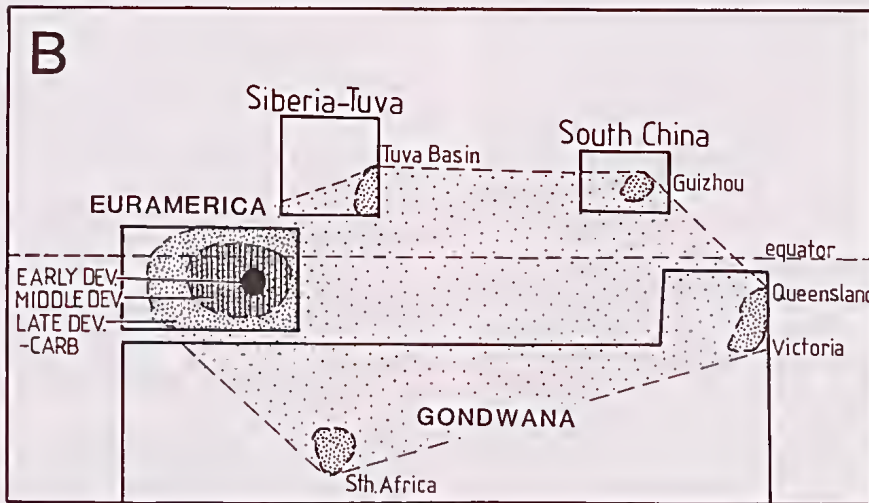
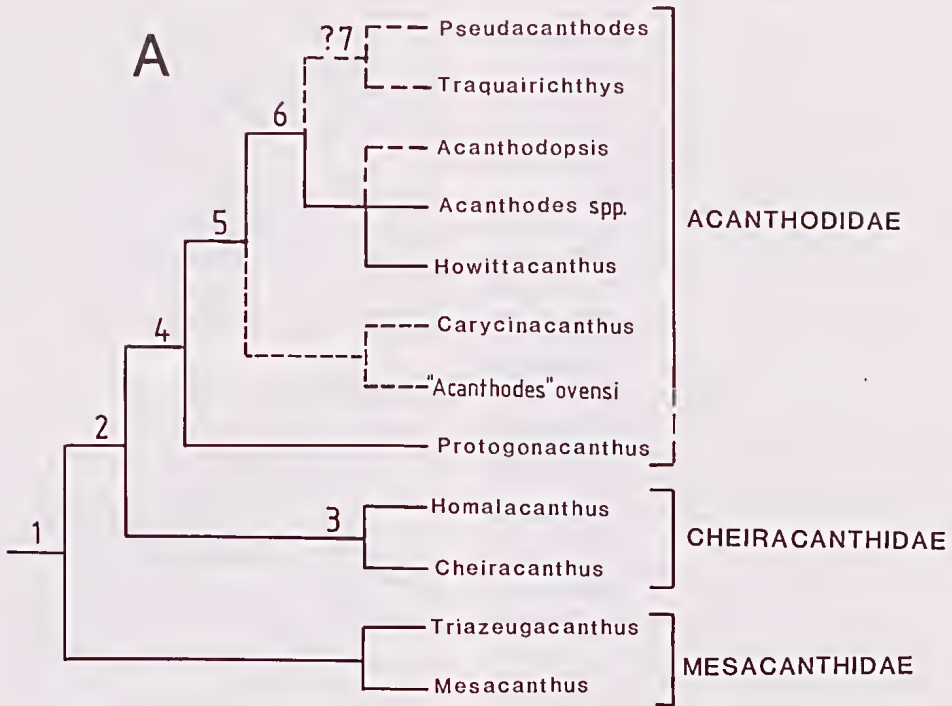


Fig. 11—A, hypothesis of acanthodiform interrelationships. Dashed lines represent tentative phylogenetic position of certain taxa for which complete anatomical data are lacking. Familial groupings according to this paper. Numbered synapomorphies: 1, single dorsal fin; scales with flat-topped unornamented crowns and *Acanthodes*-type histology (assumed for *Howittacanthus*). 2, loss of intermediate fin-spines. 3, scales with ornamented crowns; loss of mandibular splint. 4, branchiostegal rays extending only halfway across length of gill chamber. 5, fin-spines with single rib (assumed convergence with *Homalacanthus*); relatively long based pelvic fin. 6, palatoquadrate ossified in three parts; metapterygoid with both otic and auxiliary otic cotyli. ??, modification or loss of pelvic fin. B, distribution of the Acanthodidae in space and time, showing dispersal area of the higher acanthodids in the Late Devonian and Carboniferous (light stipple). Provinces (after Young 1981) indicated only to show extreme range of acanthodids.

Similarly, gyracanthid climatiforms are found in the Lower and Middle Devonian of Euramerica (including southern Europe; Denison 1979) but first become widespread in the Late Devonian and Carboniferous, where they have been recorded from South Africa (Chaloner *et al.* 1980), Antarctica (White 1968) and Australia (Woodward 1906) represented by the endemic Gondwana genus *Gyracanthides*. Ischnacanthids show no clear pattern of dispersal, and their interrelationships are poorly known (Long in press). In the Early Devonian they are found in Euramerica (Watson 1937, Miles 1973a, Bernacsek & Dineley 1977, Ørving 1957), South China (Wang Nienzhong 1984) and East Gondwana (Long in press). From the complexity of the dentition it would appear that the most specialized ischnacanthids could have been those from the Emsian of south-eastern Australia. The stem group ischnacanthids are probably represented by "Nostolepis"-type jaws from the Silurian of Oesel because of their simple construction and the primitive nature of associated "Nostolepis"-type scales (Ørving 1967, Denison 1976, 1979); and by Early Devonian taxa with simple dentition such as *Uraniacanthus* (Miles 1973a, Long in press). Similarly *Machaeracanthus*, recently discovered from the Devonian of Antarctica (Dr. G. Young, pers. comm.) represents another acanthodian which is widespread by the Middle Devonian and may have come from a group which had its origin elsewhere from Euramerica. This genus may be an ischnacanthid (Zidek 1975) which would be consistent with the occurrence of other "specialized" ischnacanthids from the Emsian of Australia (Long in press). The ischnacanthids which appear to have reached a high level of organization (from dentition alone) by the Emsian, and were known to be in East Gondwana and South China may not have originated in Euramerica as the group is known from Silurian age in Euramerica, China and Australia. Ischnacanthids might be expected to show a completely different distributional pattern from acanthodiforms or the certain climatiforms discussed here.

The distributional patterns of acanthodids, gyracanthids, and diplacanthoids is consistent with that described by Young (1981) as a generalized model for Devonian vertebrates, incorporating an episode of faunal interchange between East Gondwana and Euramerica sometime between the end of the Early Devonian and the early Late Devonian. The presence of these groups in Euramerica until the Late Devonian would imply that either a biological change occurred independently in each group (such as the invasion of saltwater) or that a geographical change occurred which affected all of these groups. Prediction of a geographical change, like the breakdown of a barrier, could be tested by the distribution of other taxonomic groups (vertebrates, invertebrates, plants). Further study of Devonian biotic distributional patterns is required.

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